FOOD SUPPLY AND PARENTAL FEEDING RATES OF HOODED WARBLERS IN FOREST FRAGMENTS

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ABSTRACT.—We tested whether Hooded Warblers (*Wilsonia citrina*) experienced a smaller food supply in small versus large forest fragments in northwestern Pennsylvania. Using 16 fragments that ranged in size from 0.7 to 214 ha, we videotaped parental feeding rates to nestlings in 35 nests and sampled arthropod abundance on 24 breeding territories. Contrary to our predictions, neither feeding rate per nestling nor arthropod abundance on breeding territories was significantly less in small (<4 ha) versus large (>150 ha) fragments. Brood loss due to starvation was rare and overall nest success was not significantly less in small fragments. Similarly, prey size delivered to nestlings and arthropod size sampled on territories did not differ significantly between fragment size classes. We conclude that Hooded Warblers breeding within small forest fragments in the northwest Pennsylvania landscape do not suffer from a relatively small food supply. *Received 20 February 2001, accepted 21 March 2002.*

Research on fragmentation of temperate forests and food availability has suggested that small forest fragments contain less prey biomass than large forests. Burke and Nol (1998) found that invertebrate biomass in leaf litter was 10 to 36 times lower in Ovenbird (*Seiurus aurocapillus*) territories located in forests with >20 ha core area (area greater than 100 m from the edge). Furthermore, randomly located quadrants in small fragments contained less than half the invertebrate biomass compared to random quadrants in large forests. In Australia, Zanette et al. (2000) found a similar reduction in food for Eastern Yellow Robins (*Eopsaltria australis*); the abundance of surface-dwelling invertebrates in two small (<55 ha) forests was half that of two large (>400 ha) forests.

Because food can limit reproductive success in passerines (Martin 1987, Rodenhouse and Holmes 1992), reductions of food caused by fragmentation should have negative consequences on reproductive success. Zanette et al. (2000) found that Eastern Yellow Robins breeding in small forests had smaller eggs and nestlings compared to birds nesting in larger forests. However, in Europe, Great Tits (*Parus major*) and Blue Tits (*P. caeruleus*) occupying small fragments had feeding rates and nesting success similar to pairs in larger forests (Nur et al. 1998).

Hooded Warblers (*Wilsonia citrina*) are small, insectivorous, Neotropical migrants with a body mass of about 11 g. They are a good species for studying the relationship of forest fragmentation and parental feeding as they are considered an area sensitive, forest interior species (Freemark and Collins 1992), and their low nests are easily located and monitored. Hooded Warblers are socially monogamous and exhibit biparental care (Evans Ogden and Stutchbury 1997). They primarily glean, hawk, and hover for a wide variety of arthropods in the understory layer of the forest (Bent 1953, Evans Ogden and Stutchbury 1994; BJMS pers. obs.) with males and females using a variety of foraging heights on the breeding grounds, particularly when provisioning young.

In this study, we tested whether feeding rate and prey size in Hooded Warbler parents were associated with fragment size in northwest Pennsylvania. Using 16 forest fragments ranging in size from 0.7 to 214 ha we videotaped parental provisioning to nestlings in 35 nests. In addition, we sampled arthropods on 24 breeding territories to determine whether arthropod abundance was related to fragment size.

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METHODS

We collected data from May through July, 1999 and 2000, in 16 forest fragments within Crawford County, northwestern Pennsylvania (centered on 41° 46'N, 79° 56'W). Forests were mature to semimature mixed hardwood deciduous and were isolated, or at most connected to other forests by narrow (<40 m wide) corridors. The mean distance to the nearest forest was 110 m (range 40–250 m). Land use between forest patches was mainly cultivated or fallow farm fields. Fragments were classified to size: small (0.7–4.0 ha, $n = 12$ fragments) or large (>150 ha, $n = 4$ fragments). In the large fragments the mean distance from the edge for all territories and nests was 257.1 m ± 145.6 SD, with 80% of the nests >100 m from the forest edge. In each fragment, 70–80% of adult birds were captured in mist nets and banded with a unique combination of plastic color bands and USGS-BRD aluminum bands.

We located nests at the nest-building, egg-laying, and incubation stages by following the sound of female vocalizations to the nest. Once located, nests were checked every 2–3 days to document hatching rates and nest success. Fledging success was calculated using the ratio of nestlings fledged to nestlings hatched. Because Brown-headed Cowbird (*Molothrus ater*) nestlings are likely to require additional food, all parasitic eggs were removed prior to hatching. Mean brood size for small fragments was 2.62 ± 1.12 SD and for large fragments 3.10 ± 1.00 SD after the removal of cowbird eggs. These means did not differ significantly (*U*-test: $U = 1.03$, Z (adjusted) = 1.26, $P = 0.21$) and in our analysis we controlled for the number of nestlings per brood by measuring feeding rates as feeding rate per nestling (feeding trips/h/nestling). After hatching, nests were monitored via video recording to determine feeding rates and prey sizes. We placed video cameras 1.0–1.5 m from the nest and feeding behavior was recorded using 2-h tapes. Parents fed at least once during all of our filming sessions. Each nest was recorded for a total of 4–6 h between 06:30 and 17:00. Evans Ogden (1994) found that time of day was not associated with feeding rates in Hooded Warblers at our study site in northwestern Pennsylvania. Hooded Warbler young fledge from the nest when they are approximately 9 days old (Evans Ogden and Stutchbury 1997) and all taping took place 5–7 days after hatching. Filming was conducted over multiple days in order to attain a mean feeding rate. All nests were taped over two of the three possible days (5–7 days old), and there was no systematic bias in age of nestling and fragment size.

While viewing the tapes, we estimated prey size in relation to bill size (Simmons and Martin 1990). Hooded Warblers have a bill size of approximately 9 mm and prey items were placed into one of five prey size categories: (1) <5 mm (2) 5–9 mm (3) 10–19 mm (4) 20–30 mm and (5) >30 mm. Hooded Warblers generally are single prey loaders; however, in the event that multiple prey items were delivered during one feeding trip, each prey item was individually placed into one of the prey size categories. After samples were categorized by size, we determined median prey size. Medians were used as a way to minimize the effect of extremely small or large prey outliers, as prey sizes varied widely. In addition, prey size was quantified as a percentage of prey items longer than 20 mm. Hooded warblers feed on a wide variety of arthropod prey including flies, ants, wasps, beetles, moths and their larvae, caddisflies, and spiders (Bent 1953; BJMS pers. obs.), therefore all types of prey were considered in our analysis.

To compliment parental feeding data and to examine the association of fragmentation with available food on breeding territories, we collected arthropod samples by sweep netting 24 breeding territories; 12 of these territories also were sampled for parental feeding rates. Using methodology similar to Young (1994), we walked along 30- to 40-m transects extending from the center of the territory. Transects were located on each of the cardinal axes (N, S, E, W) and 30 sweeps, alternating between high and low, were taken along each of the four transects. We collected samples on sunny days within a 2-week period between 08:00 and 16:00, June 2000. Samples were emptied into plastic bags at the end of each transect and then frozen. We sorted the arthropods into vials containing isopropyl alcohol. Arthropods were placed into one of five size classes used for parental feeding. We calculated total arthropod abundance as well as mean and median arthropod sizes.

Most (15 of 21) of the nests from large fragments were located in a single 150-ha fragment (Hemlock Hill), while four were in a 152-ha fragment (Berlin). We sampled one territory each in two other large fragments; to assess the validity of including these two samples in our analysis, we tested their similarity to the nests sampled in the Hemlock Hill fragment (Sokal and Rohlf 1995). For one fragment, three of four feeding variables (deliveries/h/nestling, percentage of prey >20 mm, male deliveries/h/nestling, but not female deliveries/h/nestling) fit the distribution of the Hemlock Hill fragment. For the other fragment all four variables fit the distribution. Similarly, of the three arthropod sampling variables, one fragment fit the Hemlock Hill distribution for mean arthropod size and median arthropod size, but not total arthropod abundance, while the other fragment fit the distribution for all three variables. This suggests that the large fragments that were sampled using only one nest were not outliers for the majority of measured variables.

We used the Shapiro-Wilk test to determine if data were normally distributed (Sokal and Rohlf 1995). If data were not normal after transformation, we used nonparametric tests. We used regression analysis to compare feeding behavior and arthropod sampling. If residuals were not normally distributed after transformation we used the nonparametric Spearman's rank correlation (Zar 1996). Reported values are means ± SD. Two-sample tests were one-tailed; in most cases, the directed prediction was large > small. We performed power analyses for statistically nonsignificant
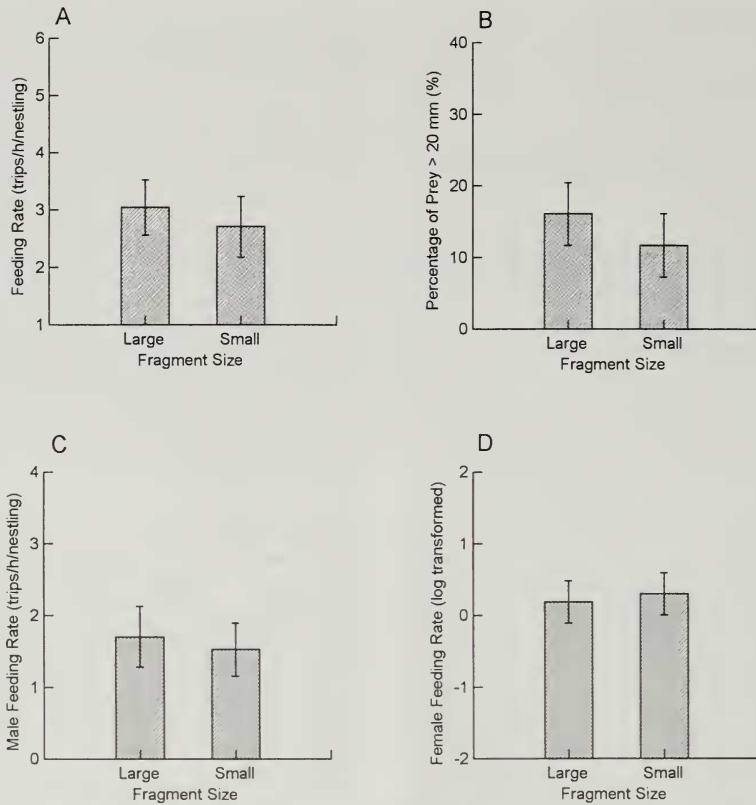
FIG. 1.   Feeding behavior of Hooded Warblers nesting in large (.150 ha) and small (<4 ha) forest fragments in Crawford County, northwest Pennsylvania, 1999–2000. (A) Feeding rate per pair. (B) Percentage of large prey. (C) Male feeding rate. (D) Female feeding rate (log transformed). Values are means and 95% confidence interval. In all cases, there were no significant differences between fragment size classes.

results because accepting the null hypothesis carries the probability of Type II experimental error. Following procedures outlined in Steidl et al. (1997) power was tested for a hypothetical difference between means of 50% at $P = 0.05$, and effect size (d) is reported with the power value while 95% confidence intervals are shown in Fig. 1. This level of difference was chosen as biologically meaningful because other studies on the relationship between forest fragmentation and parental feeding reported differences between small and large fragments of ≥50% (Burke and Nol 1998, Zanette et al. 2000).

RESULTS

We did not detect a significant difference between large and small fragments in feeding rate per pair (Fig. 1; large = 3.04 ± 1.04, $n = 21$; small = 2.71 ± 0.87, $n = 13$; $t = 0.96$, $P = 0.17$, d = 1.42, power = 0.99), male feeding rate (large = 1.70 ± 0.89, $n = 20$; small = 1.52 ± 0.58, $n = 12$; $t = 0.61$, $P = 0.27$, d = 1.04, power = 0.87), or female

feeding rate (log transformed; large = 0.18 ± 0.64, $n = 21$; small = 0.30 ± 0.46, $n = 12$; $t = -0.54$, $P = 0.30$, d = 0.9, power = 0.78). Males had higher overall feeding rates (trips/h/nestling) compared to their mates; however, the difference was not significant (paired t-test: $t = 1.30$, df = 30, $P = 0.10$). The feeding rate of males (Fig. 1C) and females (Fig. 1D) did not differ significantly between small and large fragments.

Pairs in large fragments likewise did not deliver a significantly greater percentage prey >20 mm (Fig 1; large = 16.02 ± 9.46, $n = 21$; small = 11.63 ± 7.18, $n = 13$]; $t = 1.44$, $P = 0.08$, d = 0.7, power = 0.62). During feeding trips, parents in both fragment size classes brought a wide variety of arthropod prey, including moths and their larvae, flies, beetles, and spiders.

The number of young fledged per nest was

TABLE 1. Arthropods sampled on Hooded Warbler breeding territories in large (>150 ha) and small (<4 ha) forest fragments, Crawford County, northwestern Pennsylvania, June 2000.

Variable	Large $n = 13$	Small $n = 12$	Test statistic	P
Total abundance	4.73	4.83	-0.61[a]	0.27[b]
Mean arthropod size	1.81	1.81	0.79[c]	0.22
Median arthropod size	1.65	1.87	1.24[c]	0.10

[a] t-test.
[b] $d = 1.08$, power = 0.83.
[c] S: Wilcoxon sign-rank test.

not significantly different between pairs in different fragment size classes (large = 2.57 ± 1.43, $n = 21$; small = 2.46 ± 1.27, $n = 13$; Wilcoxon sign-rank test: $S = 217.5$, $P = 0.72$) and partial brood loss attributed to starvation occurred in only one nest (in a 2.0-ha fragment). Regardless of fragment size, fledging success was not correlated with feeding rates per nestling (Spearman's rank correlation: $r_s = 0.202$, $n = 34$, $P = 0.25$). An insignificant difference in brood parasitism, measured by the number of cowbird eggs per nest, was found between fragment size classes (large = 0.48 ± 0.60, $n = 21$, small = 0.46 ± 0.52, $n = 13$, $S = 229$, $P = 0.97$).

Sweep netting indicated that none of the variables associated with arthropod size and abundance were significantly higher on territories in large fragments compared to those in small fragments (Table 1). However, in both small and large fragments arthropods >20 mm (size categories 4–5) were significantly less abundant than arthropods <20 mm (size categories 1–3) (t-test; small: $t = 9.46$, 11 df, $P < 0.0001$; large: $t = 6.27$, 12 df, $P < 0.0001$).

We examined if feeding rates per nestling were associated with arthropod abundance and size by comparing instances where both sweep netting and feeding behavior were sampled from the same territory ($n = 12$). Feeding rate per nestling was not significantly correlated with total abundance ($r^2 = 0.03$, $t = 0.58$, $P = 0.24$), or mean size class found on territories ($r^2 = 0.06$, $t = 0.81$, $P = 0.22$). The median prey size delivered to young was significantly larger than the median prey size sampled via sweep netting (two-tailed paired t-test: $t = -4.80$, 11 df, $P = 0.0003$).

DISCUSSION

This study is one of the first to investigate the relationship of fragmentation and parental feeding and food abundance. Our results indicate that Hooded Warblers breeding in small (<4 ha) fragments in northwestern Pennsylvania did not have a significantly lower feeding rate compared to pairs breeding in large (>150 ha) fragments over the years we studied. Furthermore, systematic arthropod sampling showed that small fragments did not have a significantly fewer or smaller arthropods. Our results are in contrast to those of Burke and Nol (1998) and Zanette et al. (2000). Burke and Nol (1998) found 10–36 times less leaf litter biomass on Ovenbird territories located in small fragments (>20 ha core area). Zanette et al. (2000) found that invertebrate biomass in small fragments was less than half of that found in large fragments. Power analysis demonstrates that our sample sizes were sufficient to detect differences of the magnitude found in these previous studies.

Relative to Ovenbirds and Eastern Yellow Robins, Hooded Warblers exhibit different space use patterns in forest strata. Ovenbirds forage primarily on the forest floor (Holmes and Robinson 1988) and Eastern Yellow Robins also capture invertebrates on the ground (Marchant 1986). The ground arthropods taken by these species can be susceptible to soil and leaf litter desiccation near forest edges (Matlack 1993). In contrast, Hooded Warblers are primarily gleaners (Evans Ogden and Stutchbury 1997) and increased light intensity near forest edges may have no effect on or actually increase the overall abundance of prey (Ferguson 2000, McGeoch and Gaston 2000). In the only other study to examine food supply of gleaning species, Nur et al. (1998) failed to find a relationship between Great Tit and Blue Tit feeding rates and fragment size.

Similar to the study of tits (Nur et al. 1998), we did not find higher feeding rates or larger prey items in large fragments. Despite this finding, it is possible that lower quality food (i.e., energy content or nutrition) is dependent upon fragment size. To investigate this idea, daily measurements of nestlings from hatching to fledging is needed. We know that parents did not compensate for less food by leaving small fragments in search of food because

radio-tracking studies in the same study site showed that Hooded Warbler females rarely left their territory fragment (Norris and Stutchbury 2002), and although males do leave fragments, these movements are primarily for extrapair copulation forays rather than foraging (Norris and Stutchbury 2001). However, parents may compensate for lower food availability with a higher feeding effort, thus spending more time provisioning young and less time in alternate activities. To investigate feeding effort an examination of adult activities while not feeding, and parental body condition and survivorship is needed.

Few studies have examined the relationship of forest fragmentation with arthropod abundance through direct arthropod sampling. Our sweep netting data indicated that none of the variables associated with arthropod size and abundance were significantly higher on territories in large fragments compared with those in small fragments. Our power analyses show that if differences do exist, they are modest and not of the magnitude detected by Burke and Nol (1998) and Zanette et al. (2000). Our findings are in accordance with a recent study by Sekercioglu et al. (2002) in which extensive sampling of invertebrate communities and avian diets revealed no important difference between large and small tropical fragments. The arthropod samples give an independent measure of whether food availability differs between fragment size classes. We know that Hooded Warblers forage extensively in the 2 m of understory where we sampled (Bent 1953; BJMS pers. obs.), and we found no significant difference in Hooded Warbler feeding rate, suggesting that food availability in general is not different.

In this study we sampled a wide variety of small fragments, but most of the pairs sampled in the large fragments came from a single forest, which limits the generality of our results (Hurlbert 1984). We minimized this bias by sampling pairs from throughout this fragment, which contained heterogeneous habitat types (primarily deciduous forest with heavy understory versus mixed coniferous/deciduous with light understory) and through a range of Hooded Warbler densities (see Tarof et al. 1998). Also, sampled nests included those in the center of the fragment and those near edges, and this fragment was of a size typical in

this landscape. Furthermore, our small fragments were <4 ha, smaller than the forests sampled by Burke and Nol (1998) and Zanette and et al. (2000), suggesting we had a high probability of detecting edge effects if they were present.

Although edge effects are thought to cause a large reduction in food availability for forest birds (Burke and Nol 1998, Zanette 2000), our study, along with those of Nur et al. (1998) and Sekercioglu et al. (2002), suggest that this is not always the case. Clearly, to understand whether habitat selection and nesting success of forest birds in fragmented landscapes is influenced directly by food availability, more studies need to be conducted on species with various foraging behaviors.

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